

УДК 594.3

EVALUATION OF ANATOMICAL CHARACTERS AND THEIR APPLICABILITY FOR RECONSTRUCTING PHYLOGENETIC RELATIONSHIPS IN THE PALAEARCTIC SPECIES OF *PISIDIUM* S. L. (MOLLUSCA, BIVALVIA)

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Accepted 2 September 1997

Evaluation of anatomical characters and their applicability for reconstructing phylogenetic relationships in the Palaearctic species of *Pisidium* s. l. (Mollusca, Bivalvia). Korniushev A. V. — Anatomical study of the small clams traditionally included in the genus *Pisidium* revealed new taxonomically and phylogenetically significant characters. Plesio- and apomorphic states are determined for these characters whenever possible. Synapomorphies in anatomical characters support some intrageneric groups established earlier and encourage to suggest the new affinities between species.

Key words: anatomy, *Pisidium*, phylogeny, Palaearctic

Значимость анатомических признаков для реконструкции филогенетических отношений видов рода *Pisidium* s. l. (Mollusca, Bivalvia) фауны Палеарктики. Корнишев А. В. — Исследование анатомии мелких двусторчатых моллюсков, традиционно включаемых в род *Pisidium*, выявило новые таксономически и филогенетически значимые признаки. Определены плезиоморфные и апоморфные состояния этих признаков. Синапоморфии по анатомическим признакам подтверждают монофилию некоторых внутриродовых группировок, установленных по конхологическим признакам, и выявляют неизвестные ранее родственные связи между видами.

Ключевые слова: анатомия, *Pisidium*, филогения, Палеарктика

Introduction. Palaearctic fauna of the smallest freshwater clams traditionally included in the large genus *Pisidium* is rather well known, since several review papers were published (Zeissler, 1971; Stadnichenko, 1984; Piechocki, 1989 et al.). At the same time, reliable data on phylogenetic relations of species represented in this region are still lacking. The main reason is scarcity of taxonomic characters available to earlier reviewers. Among the first attempts to present phylogeny of the group, the paper of Meier-Brook (1986) is the most notable.

In the course of anatomical studies carried out by the author (1990, 1992, 1995a, b, 1996a, b, 1997a, b), new taxonomically significant characters were found. These characters were reviewed most completely in the recently published monograph (Korniushev, 1996b). However, the obtained results appeared to be largely unavailable to the majority of the malacological community because of incompatibility of the system accepted in the countries of the former Soviet Union and based on the ideas of the "Leningrad-School" (Starobogatov & Streletskaja, 1967; Pirogov & Starobogatov, 1974; Korniushev, 1990, 1992) and that used in Western countries (Kuiper, 1962). The principal differences between the mentioned systems concern the number of species recognized as valid and the ranks of higher taxa. Discussion between the supporters of different taxonomic approaches has lasted for several decades and this is not the place here for details. In these circumstances, it seems very important to resume mutual understanding between specialists from different countries and therefore attempts to interpret the new morphological data in the framework of traditional taxonomic approach were undertaken (Korniushev, 1995a).

Application of the new anatomical characters for taxonomy is also hindered by lack of their phylogenetic interpretation. A variety of states was described in the characters of mantle, gill, brood pouch and nephridium (Korniushev, 1992 et al.), but the use of Hennigian approach, proved to be a reliable theoretical basis for phylogenetic analysis in the course of last decades (Meier-Brook, 1986), was rather limited.

The principal purpose of this paper is to show applicability of the anatomical characters for phylogenetic analysis. Plesio- and apomorphic states were defined whenever possible. These results provided additional support for the grouping outlined in earlier publications and encouraged to suppose some other taxo-

nomic affinities. Thus, application of anatomical data in the phylogenetic investigation of *Pisidium* seems to be rewarding.

However, some patterns of the constructed trees are still not clear. Taxonomic ranks of the intragenetic groups distinguished within *Pisidium s.l.* are not defined for this reason. Complete phylogenetic analysis using all available characters of shell and anatomy as well as relevant computer software is planned for the next stage of research.

Material and Methods. This paper is based on materials reviewed in the mentioned monograph (Korniushin, 1996b), therefore no collection details are presented here. For the reasons explained in the Introduction, traditional view on species delimitation is accepted in this paper (contrary to my earlier publications) and the genus *Pisidium* is interpreted in the broadest sense (Kuiper, 1962). In order to stress on the broad understanding of the genus, the designation *Pisidium s. l.* is used. The list of the species studied is provided below:

<i>Pisidium amnicum</i> (Müller, 1774)	<i>P. henslowanum</i> (Sheppard, 1823)
<i>P. moitessierianum</i> Paladilhe, 1866	<i>P. supinum</i> A. Schmidt, 1851
<i>P. tenuilineatum</i> Stelfox, 1918	<i>P. lilljeborgi</i> Clessin, 1886
<i>P. stewarti</i> Preston, 1909	<i>P. waldeni</i> Kuiper, 1975
<i>P. dancei</i> Kuiper, 1962	<i>P. subtruncatum</i> Malm, 1855
<i>P. subtilestriatum</i> Lindholm, 1909	<i>P. pulchellum</i> Jenyns, 1832
<i>P. personatum</i> Malm, 1855	<i>P. nitidum</i> Jenyns, 1832
<i>P. casertanum</i> (Poli, 1791)	<i>P. pseudosphaerium</i> Favre, 1927
<i>P. globulare</i> Clessin in Westerlund, 1873	<i>P. milium</i> Held, 1836
<i>P. obtusale</i> (Lam., 1818)	<i>P. hibernicum</i> Westerlund, 1894
<i>P. hinzi</i> Kuiper, 1975	<i>P. conventus</i> Clessin, 1877

Applicability of generic and subgeneric units proposed by Russian taxonomists alongside those widely accepted in the West is discussed, but their rank is not determined. *Pisidium globulare* is considered distinct species because of the peculiarities of its gill structure and development (Korniushin, 1996b, 1997a).

The methods of anatomical study were also described elsewhere (Korniushin, 1992, 1995b, 1996b). While analysing anatomical characters, I followed the scheme of Meier-Brook (1986) and Mansur & Meier-Brook (1992). The trends of evolution was observed for each of the studied characters and probability of parallelism was evaluated. The characters proved to be the most informative from this point of view were selected for the further analysis. Identification of plesio- and apomorphic states was based mainly on the outgroup criterion; the proper outgroups were selected for each level of analysis. All cladograms presented in this paper were constructed "by hand". Phylogenetic software was not used at this stage because of limited number of selected characters.

Results and Discussion

Evaluation of taxonomic characters. The shell. Only the principal shell characters which have considerable influence on anatomy are observed here. The most remarkable trend of shell evolution is the diminution of size (Boettger, 1961). Posterior position of umbo, peculiar for the species of *Pisidium s. l.*, is not common among bivalves, therefore might be a synapomorphy of the mentioned group. However, some cases of posterior shift of umbo in *Sphaerium s. lato* species are known: Kuiper & Hinz (1984) demonstrated this feature for *Sphaerium forbesii* (Philippi) and Korniushin (1995b) for *Musculium inomitatum* (Kuiper). Since the species mentioned live on different continents (in South America and Africa respectively) and are different in many other characters, the similar position of umbo in them should be regarded as parallelism. Thus, parallel development of this character in *Pisidium s. l.* also cannot be excluded.

Type of ligament has been applied in taxonomy of *Pisidium s.l.* by Kuiper (1962) as a crucial taxonomic character for subgeneric division. The principal types of ligament are: exterior (subgenus *Afropisidium* Kuiper), enclosed (*Pisidium s. str.* and *Neopisidium* Odhner), and introverted (*Odhneripisidium* Kuiper). However, Meier-Brook (1994) mentions that some transitional types of ligament are distinguishable in *Pisidium*, especially in *P. (N.) moitessierianum* and *P. (O.) tenuilineatum*. Thus, char-

acters of ligament need more careful investigation, but it is clear now that their value should not be over-estimated.

Mantle. Arrangement of siphons is also a character already in use (Odhner, 1921; Kuiper, 1962). Distinguished are the 3 types: *Sphaerium* s. l. species have two long tubular siphons, most of the *Pisidium* species – the short funnel-like anal siphon and a branchial opening; the species belonging to subgenera *Neopisidium*, *Odhneripisidium* and *Afropisidium* – only the rudimentary anal siphon.

Arrangement of siphonal retractors described by Korniushev (1992) can also be applied in phylogeny. The general plan of siphonal musculature (one pair of retractors for the anal siphon, 1 or 2 pairs for the branchial one) was not found elsewhere and seems to be a good apomorphy for the large group (family or superfamily) including *Eupera*, *Sphaerium*, *Musculium*, and *Pisidium*. As to the branchial siphon retractors, the historical sequence of states can be reconstructed as follows: branchial siphon with 2 pairs of retractors (*Eupera*, *Sphaerium*, *Musculium*), branchial opening with 1 pair of

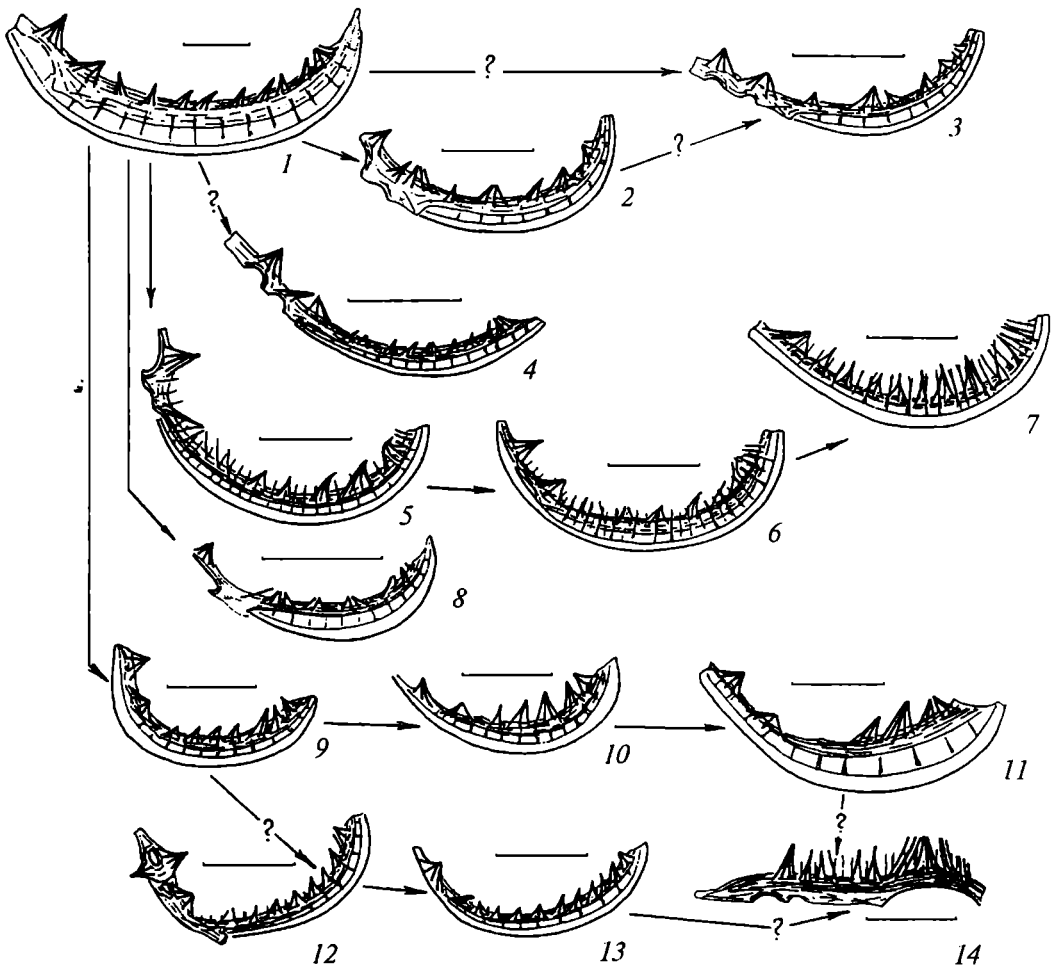


Fig. 1. Probable evolutionary transitions between the types of mantle musculature in *Pisidium* s. l.: 1 – *P. casertanum* (initial type), 2 – *P. personatum*, 3 – *P. obtusale*, 4 – *P. hibernicum*, 5 – *P. lilljeborgi*, 6 – *P. henslowanum*, 7 – *P. supinum*, 8 – *P. conventus*, 9 – *P. pulchellum*, 10–11 – *P. subtruncatum*, 12 – *P. nitidum*, 13 – *P. pseudosphaerium*, 14 – *P. milium*. Scale bar 1 mm.

retractors (most of *Pisidium s. l.*), joining of the branchial opening to the pedal slit with retaining a pair of retractors (*P. moitessierianum* + *P. (Afropisidium) spp.* + *P. (Odhneripisidium) spp.*). Parallel reduction of siphons probably took place in *P. conventus*. Position of the branchial siphon retractors (in this species they are rudimentary) indicates that branchial opening was overgrown by the presiphonal suture of mantle (for details see Korniusshin, 1996b).

The long pre-siphonal fusion (suture) of mantle was first noticed in some species of *Pisidium* by Odhner (1929). Meier-Brook (1986) considered it a synapomorphy for *P. pulchellum*, *P. subtruncatum*, *P. pseudosphaerium* and *P. milium*. However, this condition was found in *P. nitidum* as well (Korniusshin, 1992).

The author has demonstrated that elongation of the suture is associated with certain rearrangement of the pedal slit musculature, particularly of the inner radial muscle bundles. Probable evolutionary relationships between the types of the mantle muscles arrangement are shown in the Fig. 1.

The following condition is the most common in *Sphaerium*, *Musculium*, and *Pisidium* (found in *P. amnicum*, *P. subtilestriatum*, *P. casertanum*) (Fig. 1, 1): no shortening of pedal slit, many bundles of equal size evenly arranged along its edge. The mentioned groups are not closely related and thus the described condition well represents plesiomorphic state. Principal derived conditions found in *Pisidium s. l.* are the following:

- concentration of muscles in a few bundles with the strongest ones being placed in the middle part of pedal slit: *P. personatum*, *P. hinzi*, *P. obtusale* (Fig. 1, 2-3); the similar pattern is observed in *P. conventus* (Fig. 1, 8);
- general reduction of inner radial mantle muscles with desintegration of their bundles, especially in the posterior section of pedal slit: *P. lilljeborgi*, *P. henslowanum*, *P. supinum* (Fig. 1, 5-7);
- strong anterior concentration of muscles due to elongation of pre-siphonal fusion: *P. pulchellum* and *P. subtruncatum* (Fig. 1, 9-11);
- elongation of pre-siphonal fusion followed by some reduction of inner radial muscle bundles and their even concentration along the pedal slit: *P. nitidum*, *P. pseudosphaerium* (Fig. 1, 12-13); this condition may be derived from that taking place in *P. pulchellum* where anterior concentration of muscles is not so advanced as in *P. subtruncatum*.

The case observed in *P. milium* is similar to that of *P. subtruncatum* in a very short pedal slit and strong concentration of muscles. However, no anterior shift of bundles (so peculiar in *P. subtruncatum*) is visible (Fig. 1, 14). In this aspect, the "milium" type of musculature is more related to that occurring in *P. nitidum* and *P. pseudosphaerium*, and probably might originate from the common ancestor of these species.

Considerable reduction of muscle bundles takes place in *P. hibernicum* as well. However, the pattern of their arrangement is quite specific and its independent development is highly probable (Fig. 1, 4).

Gills. It is assumed usually that general trend of ctenidium evolution in sphaeriids is reduction (Meier-Brook, 1970). Korniusshin (1996a) suggested to evaluate the outer demibranch reduction quantitatively, by counting filaments between the anterior edges of the inner and outer demibranchs. Statistically significant differences in these characters were found between many species of *Pisidium s. l.* (Korniusshin, 1997a).

Heterogeneity of gill characters within *P. casertanum* is also notable (Korniusshin, 1997a). In particular, the form identified with *Pisidium globulare* Clessin is distinguished by large outer demibranch, which makes it possible to suppose specific status of the latter.

It is also important that in *P. amnicum* the outer demibranch is much more reduced than in *P. subtilestriatum*; it is more shifted posteriorly and appears later in on-

togenesis (Korniushtin, 1996a, 1997a). The second lamella of the outer demibranch is constantly present in *P. subtilestriatum*, but not in *P. amnicum* (Korniushtin, 1996b).

It is generally assumed, that the more reduced is outer demibranch – the more advanced is the phylogenetic position of the taxon. From this I conclude, that the initial (ancestral) position of the outer demibranch in *Pisidium s.l.* is at the 7th or 8th filament of the inner one. This condition is the most common and occurs in *P. subtilestriatum*, *P. obtusale*, *P. henslowanum*, *P. hibernicum*, *P. nitidum* and *P. pseudosphaerium* (Korniushtin, 1997a). This seems to be an important apomorphy, because in *Sphaerium* and *Musculium* the outer demibranch begins at the 5th filament of the inner one (Korniushtin, 1996a, 1997a). Parallel reduction of gills in less closely related taxa is highly probable. It is shown, that the outer demibranch in *P. globulare* appears in rather late stages of development (Korniushtin, 1996a) and in the course of ontogenesis evidently enlarges anteriorly. Therefore, the conspicuous size of the organ should be considered in this case an apomorphy.

Complete reduction of the outer demibranch is observed in the group, described by Odhner (1921) as a subgenus *Neopisidium*. Heterogeneity of the siphonal muscles patterns and brood pouch arrangement (see below) in this group indicate, that in *P. conventus* reduction occurred independently from the other species.

Brood pouch. Taxonomic significance of this organ was first analysed by Meier-Brook (1970), who discovered different locations of brood pouch anlagen in *Pisidium s. l.* Korniushtin (1992) distinguished between 4 types of brooding in Pisidiidae. Euperid type (incubation of large eggs in the inter-lamellar space without any brood pouch) was considered an ancestral, pisidiid (one brood pouch in the upper part of inner demibranch), euglesid (one pouch, but with lower position) and sphaeriid (several brood pouches) types being derived from that. The latter type was considered to be the most advanced. On the contrary, Mansur & Meier-Brook (1992) considered the multi-pouch condition of *Sphaerium* and *Musculium* plesiomorphic.

It is necessary to mention that *P. amnicum* and *P. subtilestriatum* considered closely related since Odhner (1940) have different types of brood pouches: in the latter species they are of euglesid, not of pisidiid type.

Some new facts were revealed in the meantime. Oogenesis in *Eupera* appeared to be quite peculiar (Mansur & Meier-Brook, in press), there was no evidence that *Sphaerium* had such an ancestor. Simultaneous incubation of several broods without formation of brood pouch (in the interlamellar space of the inner demibranch) was discovered in corbiculids, namely in *Neocorbicula limosa* (Maton) (Ituarte, 1994). Close relationship between corbiculids and sphaeriids is still not evident (Mansur & Meier-Brook, 1992) and we do not think that the latter might originate from *Neocorbicula*. But parallel evolution of breeding habits in 2 families seems to be very probable and the common ancestor of *Sphaerium* and *Pisidium* might have the mode of brooding similar to that in the mentioned species. The sphaeriid type might develop on this base and thus should be considered plesiomorphic. The other argument in favour of plesiomorphic nature of this state is that it is always associated with plesiomorphic condition of siphons and gills (in *Sphaerium* and *Musculium*). Transition from the multi-pouch state to the uni-pouch one might be caused by size reduction, as supposed by Meier-Brook (1970).

Despite the different views on evolution of the brooding organs, Meier-Brook (1970) and Korniushtin (1992) agreed that the upper position of the brood pouch anlage described in *Pisidium amnicum*, *P. moitessierianum*, *P. (Afropisidium)* and *P. (Odhneripisidium)* species, is plesiomorphic in respect to the lower position common to other *Pisidium s.l.* In the light of the new hypothesis presented here, another aspect of the problem appears. The lower position is similar to that in *Sphaerium* and *Musculium* and may be derived from such directly. If this is true, then the lower position of the brood pouch anlage is plesiomorphic. Thus, the apo/plesiomorphic condition in

position of the brood pouch anlage cannot be determined with certainty. This problem needs further investigation.

Peculiar brood sac structure (only each 2nd filament contributes to its formation) was noticed in *P. henslowanum* and *P. lilljeborgi* by Odhner (1929). Meier-Brook (1970, 1986) considered condition observed in these two species unique in the genus and that's why regarded it as an apparent apomorphy. However, Korniuschin (1992) found it also in *P. amnicum* and *P. subtilestriatum* and concluded that it should be a plesiomorphy. Alternating filament participation in the brood sac in *P. amnicum* and *P. subtilestriatum*, as well as in *P. supinum* and *P. waldeni*, was confirmed by Korniuschin (1996b). Despite the primitive state of many characters in *P. amnicum* and *P. subtilestriatum*, I assume that arguments for plesiomorphic nature of their filament arrangement are not sufficient. Convergent evolution of this condition is highly probable.

Nephridium. Taxonomic and phylogenetic significance of nephridium characters is discussed by Mansur & Meier-Brook (1992) and Korniuschin (1997b). Remarkable similarity between *Musculium* and *Pisidium* s. l. should be mentioned in this respect. The distinct type of nephridium with the lateral loop lying on the dorsal surface reported for *P. moitessierianum*, *P. (Afropisidium)* and *P. (Odhneripisidium)* (Korniuschin, 1997b) is probably an apomorphy in respect to that known for the majority of *Pisidium* s. l. Some other similarities and differences in the dorsal lobe characters between species were also described by the author. Distinguished were the closed type of nephridium with the branches of dorsal lobe tightly adjoining each other and the open one where a small part of pericardial tube is visible between these branches. The first type was considered a plesiomorphic state in *Pisidium* s. l. (Korniuschin, 1997b). Some differences in proportions of the dorsal lobe were noted. It is evident, that configuration of the dorsal lobe may provide additional support for grouping, but plesiomorphic vs apomorphic state in this case can hardly be decided on.

The anatomical data presented above are summarized (with a certain degree of simplification) in the following list:

I. Subgeneric characters:

1. Siphons: 1.1 – two siphons, both tubular, 1.2 – upper (anal) siphon and a branchial opening, 1.3 – branchial opening merged to the pedal slit;
2. Siphonal musculature: 2.1 – three pairs of retractors (a pair by the anal siphon and two pairs by the branchial one), 2.2 – two pairs of retractors (one pair by each opening);
3. Structure of outer demibranch: 3.1 – both lamellae (inner and outer) normally developed, 3.2 – inner lamella reduced, 3.3 – only outer lamella present, 3.4 – outer demibranch absent;
4. Brood pouches: 4.1 – multiplied pouches (sphaeriid type), 4.2 – single pouch;
5. Brood pouch position: 5.1 – upper (pisidiid type), 5.2 – lower (euglesid type);
6. Position of nephridium lateral loop: 6.1 – ventral, 6.2 – latero-dorsal.

II. Specific characters:

1. Presiphonal suture: 1.1 – short, 1.2 – elongated;
2. Development of inner radial muscles: 2.1 – strong bundles, 2.2 – weak bundles, 2.3 – profound reduction with desintegration of some bundles;
3. Arrangement of muscle bundles: 3.1 – even, 3.2 – concentration in the middle part of mantle, 3.3 – concentration in the anterior part, 3.4 – concentration in two large bundles;
4. Position of outer demibranch: measured by ordinal number of the inner demibranch filament corresponding to the anterior edge of the outer demibranch;
5. Structure of brood pouch: 5.1 – each filament contributes to its formation, 5.2 – only each second filament contributes;
6. Type of nephridium: 6.1 – closed, 6.2 – open;
7. Proportions of the dorsal lobe: 7.1 – elongated, 7.2 – square, 7.3 – broad.

Phylogenetic implications. 1. Relations between the major subgroups of *Pisidium* s. l. Character states found in these taxa are shown in the Table 1. Genus *Musculium* regarded as a sister taxon of *Pisidium* s. l. by Mansur & Meier-Brook (1992) was selected as an outgroup for this analysis. The group under consideration is characterized by reduced state of several organs and structures: mantle edge and its musculature, gills and brood pouches (Table 1, Fig. 2). Repetition of each reduction is

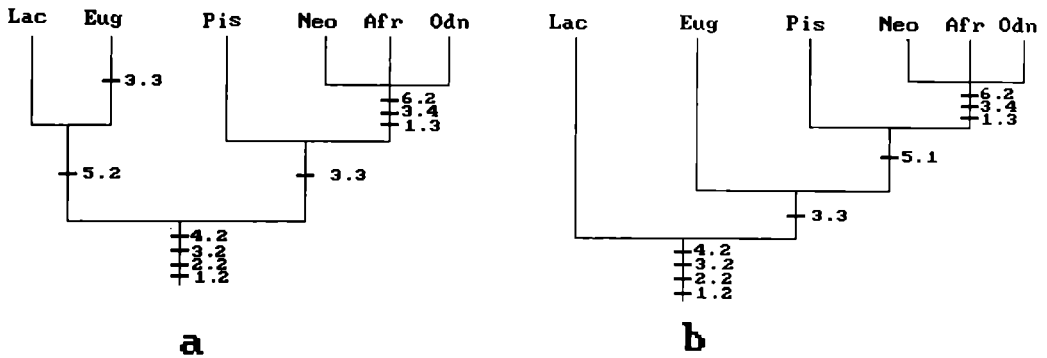


Fig. 2. Phylogenetic relations of the major groups distinguished within *Pisidium* s. l.: Lac — *Lacustrina*, Eug — *Euglesa*, Pis — *Pisidium* s. str., Neo — *Neopisidium*, Afr — *Afropisidium*, Odn — *Odhneripisidium*; Principal apomorphies are shown, their numbers correspond to those in the Table 1.

Table 1. States of anatomical characters in subgeneric groups distinguished within *Pisidium* s. l. (the first figure is the number of character, the second indicates its state, explanations are in the list of characters)

Characters	1	2	3	4	5	6
<i>Musculium</i> (outgroup)	1.1	2.1	3.1	4.1	5.2	6.1
<i>Lacustrina</i>	1.2	2.2	3.2	4.2	5.2	6.1
<i>Euglesa</i>	1.2	2.2	3.3	4.2	5.2	6.1
<i>Pisidium</i> s. str.	1.2	2.2	3.3	4.2	5.1	6.1
<i>Neopisidium</i>	1.3	2.2	3.4	4.2	5.1	6.2
<i>Odhneripisidium</i>	1.3	2.2	3.4	4.2	5.1	6.2
<i>Afropisidium</i>	1.3	2.2	3.4	4.2	5.1	6.2

possible, but parallel development of their peculiar combination seems to be improbable, thus monophyly of *Pisidium* s.l. is well supported. As shown above, it is not clear now which position of the brood pouch (upper or lower) represents apomorphic state. Therefore, two different cladograms on subgeneric level are proposed. If the pisidiid type is plesiomorphic, we have 2 sister groups (Fig. 2a). One group comprises *P. amnicum* and *P. moitessierianum*, together with *Odhneri-* and *Afropisidium*. Here only the reduced descending lamella of outer demibranch might be a synapomorphy, but the same state should independently derive in the other group (*Euglesa*). If one excludes *P. amnicum*, the remaining group will be well defined by reduction of the outer demibranch, merging of branchial opening with the pedal slit and a peculiar type of nephridium. The other large group includes *P. subtilestriatum*, all traditional species of *Eupisidium* (sensu Odhner, 1940) and *P. conventus* and is defined by the lower position of brood pouch.

If the lower position of the brood pouch (euglesid type of breeding) is a plesiomorphy (Fig. 2b), then *P. subtilestriatum* with its well developed outer demibranch would become a sister group of that group which includes all the remaining species. In this case, upper position of the pouch would be a good synapomorphy for the group including *P. amnicum*, *Neopisidium* and related taxa.

In the both cases, we have four major species groups (subgenera or even higher taxa), with their relationships not yet clarified. *Pisidium* s. str. is represented in Palearctic only by *P. amnicum*. The next group includes species of the following subgenera in the sense of Kuiper (1962): *Neopisidium* (except *P. (N.) conventus*), *Odhneripisidium* and *Afropisidium*. If accept Boettgers (1961) point of view on type species designation in *Neopisidium*, the latter name is available for the whole group.

Contrary to the cladograms suggested by Meier-Brook (1986), I consider the group including *P. subtilestriatum* and North American *P. idahoense* Roper not closely related to *P. amnicum*. Distinct phylogenetic position of the first two species is supported by the larger size of the outer demibranch, presence of second lamella in it and lower position of the brood pouch. *P. idahoense* is the type species of *Lacustrina* Sterki, which may be attributed to the group as a generic or subgeneric name (Starobogatov & Streletskaia, 1967). It is necessary to mention here, that identity of *P. di-*

Table 2. States of anatomical characters in species of the group *Euglesa* (character 4 is the number of filament where outer demibranch anterior edge is placed, other designations are the same as in the character list)

Characters	1	2	3	4	5	6	7
<i>Pisidium subtilestriatum</i> (outgroup)	1.1	2.1	3.1	7-8	5.2	6.1	7.1
<i>P. casertanum</i>	1.1	2.1	3.1	10-15	5.1	6.1	7.2
<i>P. globulare</i>	1.1	2.1	3.1	5-6	5.1	6.1	7.2
<i>P. personatum</i>	1.1	2.1	3.2	8-12	5.1	6.1	7.2
<i>P. obtusale</i>	1.1	2.1	3.2	8-10	5.1	6.1	7.2
<i>P. hinzi</i>	1.1	2.1	3.2	7-8	5.1	6.1	7.2
<i>P. nitidum</i>	1.2	2.2	3.2	7-8	5.1	6.2	7.3
<i>P. pseudosphaerium</i>	1.2	2.2	3.2	7-8	5.1	6.2	7.2
<i>P. milium</i>	1.2	2.1	3.4	9-11	5.1	6.2	7.3
<i>P. subtruncatum</i>	1.2	2.1	3.3	9-11	5.1	6.1	7.3
<i>P. pulchellum</i>	1.2	2.1	3.3	9-11	5.1	6.1	7.3
<i>P. hibernicum</i>	1.1	2.2	3.1	7-8	5.1	6.1	7.2
<i>P. henslowanum</i>	1.1	2.3	3.1	7-9	5.2	6.2	7.2
<i>P. supinum</i>	1.1	2.3	3.1	7-9	5.2	6.2	7.2
<i>P. lilljeborgi</i>	1.1	2.2	3.1	8-11	5.2	6.2	7.2
<i>P. waldeni</i>	1.1	2.2	3.1	7-9	5.2	6.2	7.2
<i>P. conventus</i>	1.1	2.2	3.2	—	5.1	6.1	7.2

latatum Westerlund, 1897 and *P. subtilestriatum* was shown (Starobogatov & Streletskaja, 1967) and in Russian literature *P. subtilestriatum* is referred to as *Lacustrina dilatata* (Westerlund).

The name for remaining group is a painful problem. The eldest available name is *Euglesa* Leach 1851 (Pirogov, Starobogatov, 1974), but it is not unanimously recognised as valid (Kuiper, 1995). A lot of other names are used in the recent literature: *Casertiana* Fagot 1892 (Adler, 1994), *Cymatocyclas* Dall 1903 (Zeissler, 1971), etc. The final decision on this matter can be made only after thorough analysis of all alternatives. Until it is completed, the group is provisionally designated below as *Euglesa* accepting this name in the sence of Pirogov & Starobogatov (1974).

2. Affinities of species within *Euglesa*. As shown above, *P. subtilestriatum* represent a distinct taxon closely related to the group observed here. Therefore it is selected as an outgroup (Table 2). Concluding from the analysis of plesio/apomorphies, the hypothetic common ancestor of *Euglesa* can be described as follows: shell relatively large, umbo near the middle position, prae-siphonal fusion of the mantle short, pedal slit with not less than 7 bundles of radial muscles, evenly arranged and of equal size; outer demibranch with one lamella, its anterior edge approximately at the 7th filament of the inner one; nephridium of the closed type, its dorsal lobe elongated or rectangular. *Pisidium casertanum* is rather similar to this groundplan, but has more reduced outer demibranchs.

Several species groups can be distinguished on different levels of affinity in the taxon under consideration. The group comprising *P. henslowanum*, *P. supinum*, *P. lill-*

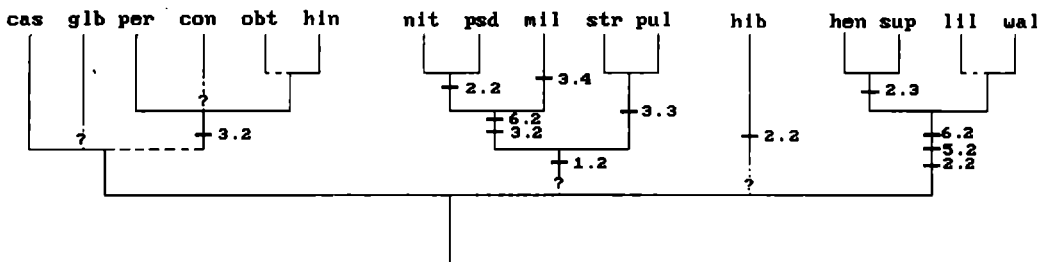


Fig. 3. Phylogenetic relations of species within the subgenus *Euglesa*: cas — *P. casertanum*, glb — *P. globulare*, per — *P. personatum*, con — *P. conventus*, obt — *P. obtusale*, hin — *P. hinzi*, nit — *P. nitidum*, psd — *P. pseudosphaerium*, mil — *P. milium*, str — *P. subtruncatum*, pul — *P. pulchellum*, hib — *P. hibernicum*, hen — *P. henslowanum*, sup — *P. supinum*, lil — *P. lilljeborgi*, wal — *P. waldeni*

jeborgi and *P. waldeni* is well defined by a peculiar structure of the brood sac, by the common trend of mantle musculature reduction and by the open type of nephridium (Table 2, Fig. 3). If this group is regarded as a taxon, the name *Henslowiana* Fagot 1892 should be attributed to it. Among the species mentioned, *P. lilljeborgi* and *P. waldeni* share plesiomorphic condition of mantle musculature (relatively strong bundles), but no reliable synapomorphies were found in these species earlier considered cosely related (Meier-Brook, 1986). In *P. henslowanum* and *P. supinum*, the bundles are especially weak, which is probably a synapomorphy (umbonal folds are the another tentative synapomorphy).

Another two well defined species pairs are *P. pulchellum* – *P. subtruncatum* and *P. nitidum* – *P. pseudosphaerium*. Each pair is characterized by some derived type of mantle musculature; the available names are *Pseudeupera* Germain 1913 and *Cingulipisidium* Pirogov et Starobogatov 1974.

P. milium has some similarities to *P. subtruncatum*, *P. nitidum* and *P. pseudosphaerium*, but its connection with the *P. nitidum* – *P. pseudosphaerium* group seems to be more probable. Besides mantle musculature discussed above, similarity in nephridium configuration should be mentioned (Korniuschin, 1997b). Thus, *P. milium* can be tentatively included in *Cingulipisidium*. All five species with the elongated mantle fusion (*P. pulchellum*, *P. subtruncatum*, *P. nitidum*, *P. pseudosphaerium* and *P. milium*) can be also connected on a certain level.

Relations between the remaining species are rather intricate. *P. obtusale* and *P. hinzi* (the group *Cyclocalyx* Dall 1903) are traditionally considered to be related with the following similarities: small inflated shell and short hinge. However, phylogenetic status of these characters was not investigated. Korniuschin (1996b) reported for both species reduced number of mantle muscle bundles. The latter character is probably an apomorphy also shared by *P. personatum*. On the other hand, *P. personatum* is similar to *P. casertanum* conchologically, variation ranges in many characters touch each other or even overlap (Korniuschin, 1996b). However, no synapomorphies were found for this pair. If the similarity between *P. personatum*, *P. obtusale* and *P. hinzi* in mantle musculature is a synapomorphy, then there is another distinct group of 4 species (*Euglesa* s.str.): *P. casertanum*, *P. personatum*, *P. hinzi* and *P. obtusale*. The distinct position of *P. globulare* should be noted, but its affinities are not defined.

No reliable affinities of *Pisidium hibernicum* can currently be defined. Having reduced muscle bundles, it shows some similarity to the group of *P. henslowanum*, but parallelism seems to be more probable in this case, as mentioned above.

The same situation is with *P. conventus*. It is characterized by lower position of brood pouch and is surely derived from a common ancestor of *Euglesa*. Relatively strong muscles of the pedal slit resemble those of *P. casertanum* and *P. personatum*. This similarity is certainly due to symplesiomorphy. Certain reduction of the muscle bundles number is probably a synapomorphy with *P. personatum* group. Profound reduction of siphons and gills observed in this species in all probability was independent from the reductions taking place in the other *Neopisidium* species, therefore it should be excluded from the mentioned subgenus and observed within the group *Euglesa*.

Since most of the species included in subgenus *Odhneripisidium* are distributed outside Palearctic, their relations are beyond the framework of this paper.

Acknowledgements. The author is greatly indebted to Dr. Claus Meier-Brook (Tropenmedizinisches Institut, Universität Tübingen) for the kind attention to this investigation and, particularly, for the numerous comments and suggestions on the manuscript and cladograms. The visit to Tübingen was facilitated by Deutsche Akademische Austauschdienst (DAAD). The work was also supported by the joint grant of the International Science Foundation and Ukrainian Government (#K23100).

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